



Influence of environmental, social and behavioural variables on the whistling of the common bottlenose dolphin (*Tursiops truncatus*)

Gabriella La Manna¹ · Nikolina Rako-Gòspic² · Michele Manghi^{1,3} · Giulia Ceccherelli^{1,4}

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Abstract

Bottlenose dolphin communication has been studied extensively. Nevertheless, the combined effect of several variables on whistle structure has yet to be clearly understood. Here, we investigated the influence of underwater noise, boat presence, behaviour, group size and calf presence on the whistles of a small population of common bottlenose dolphins (*Tursiops truncatus*). Surface behaviour and acoustic data were collected in Sardinia (Italy-Western Mediterranean Sea) between 2015 and 2017. Whistle frequency parameters (minimum, maximum, start, end frequencies and frequency range), duration, number of inflection points and number of harmonics were correlated with the ambient noise levels recorded prior to the whistle display and to behavioural and social factors by means of GAM models. Whistle frequencies varied as a function of the interaction between noise and boat presence, mainly when the noise increased at lower frequencies. Dolphin whistles also varied according to group size, which was further affected by the presence of calves, and behaviours characterised by high levels of arousal such as feeding. The study provides sufficient evidence to support that multiple factors need to be considered when investigating whistle structure as the species is capable of adopting different strategies depending on environmental, social and behavioural context. Finally, this data indicates that communication within a small population of bottlenose dolphins is vulnerable to acoustic pollution, thereby highlighting the need for further investigation into the effects of different noises on whistle structure, as well as the consistency of patterns across different populations.

Significance statement

Exploring a dolphin's ability to adapt its communication to environmental context is crucial to understanding the consequences of ocean noise increase, especially in highly anthroposised areas such as the Mediterranean Sea. This is one of the few studies that investigate how noise and boat traffic affect bottlenose dolphin whistles whilst considering the concomitant effect of other variables such as behaviour, group size and composition. We demonstrated that dolphins vary their whistles as a function of increasing noise and boat presence, group size and calf presence, and during specific behaviour which requires intense contact between individuals. Finally, the results showed that other variables should be considered to fully understand those which influence whistle structure and adaptability.

Keywords Bottlenose dolphins · Acoustic behaviour · Noise · Mediterranean Sea

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✉ Gabriella La Manna
gabriella.lamanna@gmail.com

¹ MareTerra Onlus-Environmental Research and Conservation, Regione Salondra 9, Alghero, Italy

² Blue World Institute of Marine Research and Conservation, Kaštel 24, Veli Lošinj, Croatia

³ Nauta Ricerca e Consulenza Scientifica, Strada della Carità 8, Milan, Italy

⁴ Dipartimento di Chimica e Farmacia, Università degli Studi di Sassari, Via Piandanna, 4, Sassari, Italy

Introduction

Vocal communication is essential in facilitating interactions, information exchange, activity synchronisation and behaviour coordination and becomes especially important in aquatic environments characterised by reduced light and limited range of visibility (Lammers and Oswald 2015).

In the framework of marine mammal acoustic communication studies, one of the species that has dominated the literature over the last 60 years is the common bottlenose dolphin (*Tursiops truncatus*; hereafter bottlenose dolphin; Jensen 2011). This species lives in complex fission–fusion societies, characterised by frequent group changes (Wells 2003). To maintain group cohesion, facilitate group coordination and address conspecifics, dolphins produce communication calls known as whistles (Smolker et al. 1993; Tyack 1997; Janik and Slater 1998; Janik 2000; Janik et al. 2006). Whistles are narrow-band, frequency-modulated signals, used in long-range communication, which are distinguished as signature and non-signature whistles (Caldwell et al. 1990; Janik et al. 1994; Cook et al. 2004; Janik and Sayigh 2013). A signature whistle is defined as ‘a learned, individually distinctive whistle type in a dolphin’s repertoire that broadcasts the identity of the whistle owner’ (Janik and Sayigh 2013). In the wild and freely swimming dolphins, signature whistles account for up to 70% of the overall whistles produced (Buckstaff 2004; Cook et al. 2004; Watwood et al. 2005). Signature whistles have been demonstrated to function as recognition calls used to identify the emitter, primarily produced when the animal is separated from the conspecifics (Caldwell and Caldwell 1968; Caldwell et al. 1990; Janik and Slater 1998; Sayigh et al. 2007). Conversely, the non-signature whistles, also known as variant whistles, are not characterised by individually distinctive frequency-modulated patterns (Caldwell and Caldwell 1979; Watwood et al. 2004, 2005; King et al. 2013). However, few studies have examined these whistles and their function remains poorly understood (Tyack 1986; Janik and Slater 1998).

Various studies have examined changes in the acoustic parameters and production rates of whistles in bottlenose dolphins in relation to the behavioural context (Hernandez et al. 2010; Díaz Lopez 2011; May Collado and Quinones-Lebron 2014; Rako Gospić and Picciulin 2016), stress due to separation from conspecifics (Esch et al. 2009), social structure and group composition (Heiler et al. 2016; Romeu et al. 2017) and boat presence and noise levels (Buckstaff 2004; La Manna et al. 2013; Luís et al. 2014; May Collado and Quinones-Lebron 2014; Heiler et al. 2016; Rako Gospić and Picciulin 2016; van Ginkel et al. 2017). These have recently been included as covariates in understanding whistling adaptation in dolphins (May Collado and Quinones-Lebron 2014; Heiler et al. 2016). For example, May Collado and Quinones-Lebron (2014) highlighted the importance of considering the

effect of several variables in shaping dolphin acoustic response. In fact, they found that changes in whistle parameters do not only occur as a result of the presence of boats or related noise levels, but they also depend on the behavioural state of dolphins. Furthermore, Heiler et al. (2016), using a modelling approach, found an upward shift in whistle frequency caused by boat engine noise, and also, a strong influence of behavioural state and group composition on the variation of whistle frequencies and duration.

However, to our knowledge, only a few studies have investigated the complexity of the response in dolphin whistle vocalisation in relation to the combined and simultaneous effect of environmental, social and behavioural contexts of groups (Heiler et al. 2016; Marley et al. 2017). Therefore, the focus of the present study was to clarify the combined effect of underwater noise, boat presence, surface behaviour, group size and calf presence on the whistle structure of a small population of bottlenose dolphins inhabiting Sardinian waters (Mediterranean Sea).

Methods

Study area

The study area (Fig. 1) is located off of north-western Sardinia (Italy) and extends for about 300 km² along the coast of Alghero (40.5580° N, 8.3193° E). This area is one of the most hydrodynamic zones of the western Mediterranean Sea and includes a variety of different seafloor types, from the coastal gradually graded rocky bottom and the seagrass meadows (*Posidonia oceanica*) to the detrital bottom exceeding 115 m in depth. A portion of the study area falls inside the boundaries of the Marine Protected Area ‘Capo Caccia–Isola Piana’. One of the main economic activities in this area is sea-related tourism, which leads to an increase in boat traffic during the summer, mainly due to motorised and inflatable rental boats smaller than 10 m and larger (between 10 and 35 m) motor boats used for excursions along the coast (La Manna et al. 2016). The area is inhabited by a small population of common bottlenose dolphins (*Tursiops truncatus*). Between 2008 and 2011, the estimated population size in an area of about 200 km² was 55 individuals (95% CI = 44.8 to 69.5—Díaz Lopez et al. 2013), whereas between 2012 and 2018, 121 individuals were photo-identified in an area of 300 km² (LMG unpublished data). A large portion (about 50%) of these individuals showed a high level of site fidelity, since they have been sighted repeatedly each year, through the seasons (LMG unpublished data). The population seems to be neither closed nor isolated, since between 2012 and 2018, the discovery curve of the photo-identified dolphins never reached a plateau, due to the regular entrance of new individuals (LMG unpublished data).

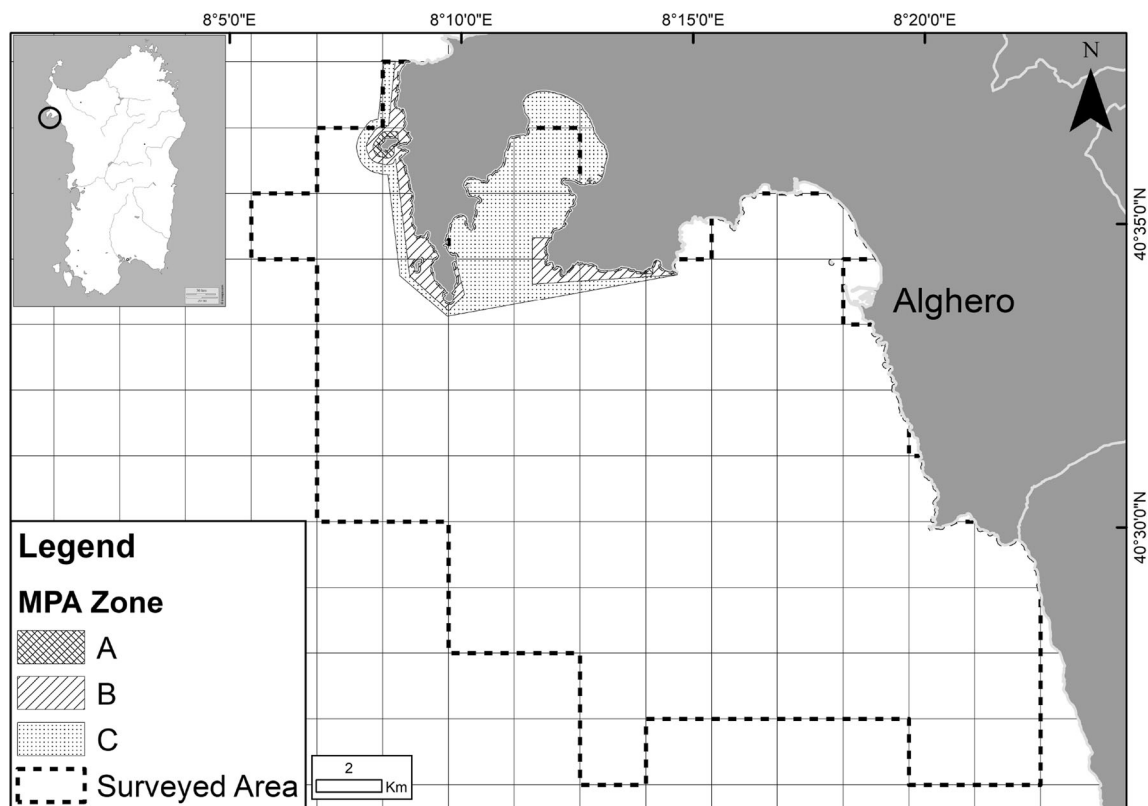


Fig. 1 Study area. Dotted line shows the surveyed area

Behavioural and acoustic data collection

Surface behavioural and acoustic data (dolphin sounds and sea ambient noise) were collected during dedicated boat surveys on a 9-m motor boat, from 2015 to 2017. At least two experienced observers scanned the sea surface at an average boat speed between 10 and 16 km per hour, during daylight and with a visibility of over 3 miles. Navigation routes were interrupted in case of sighting or when sea conditions deteriorated (sea state > 2 Douglas; wind force > 2 Beaufort). A dolphin sighting was defined as an observation of one individual or a group of dolphins. A group was defined as all individuals within visual range that were in apparent association, either by being close to each other, engaged in the same activity or moving in the same direction (Shane 1990). During each dolphin sighting, data on group size and age classes were recorded, along with photo-identification data collection. Photo-identification allows identification of each dolphin based on the presence of natural marks, nicks, scars, or skin pigmentations on the dorsal fin (Würsig and Jefferson 1990). Calves were defined as dolphins two-thirds or less than the length of an adult. Data collection began at least 20 min after the encounter started to allow the dolphins to become accustomed to the presence of the research boat. The surface behaviour of the group was recorded by following a continuous focal-group sampling (Altmann 1974; Mann 2000). It was not possible to record data blind because the study involved

focal animals in the field. Surface behaviour was assigned to one of the mutually exclusive categories (Table 1). Observations lasted between 20 and 60 min. If the members of the group displayed more than one category of behaviour, the predominant one (that performed by more than 50% of the group members) was recorded (Mann 1999). Behavioural and acoustic data were collected simultaneously by synchronising the voice and acoustic recorder turn-on. Acoustic data was recorded by means of a hydrophone (Sensor Technology SQ26-08; sensitivity 168.8 dB re 1 V/1 μ Pa; bandwidth between 10 Hz and 96 kHz) lowered to a depth of 5–10 m and connected to an M-Audio MicroTrack II or Zoom I recorder (data format 16–24-bit WAV, sampling frequency 96 kHz). Before each recording, the system was calibrated by applying a sinusoidal voltage of 100 mV RMS to the transducer input of the system by means of a signal generator. Since the identification of the whistle emitters was not possible, to avoid the risk of collecting acoustic data from a group different from the focal one, only acoustic data in presence of one group of dolphins within the visual range of the observers were recorded. During acoustic data collection, the research boat was stationed between 20 and 100 m from the group with the engine off. At the end, the number and type of boats present within 500 m of the focal group were also recorded, with the exception of the stationary ones with the engine off. Boats were categorised as follows: motor and inflatable boats, sail boats, tourist boats (diving and tour boats) and fishing boats.

Table 1 Description of the surface behavioural categories

Behavioural category	Description
Travelling	Consistent directional movement of dolphins, with regular surfacing
Resting	Slow movement of dolphins and/or floating dolphins
Socializing	Many interactive events observed, such as body contacts, pouncing and hitting with tail; many aerial events
Surface feeding	Obvious feeding activities performed close to the water surface, fish near the surface and/or aggregation of birds, and/or consistent movement following operating trawler
Milling	No net movement, individuals surface facing different directions, dive intervals variable but short

Dolphin whistle analysis

Raven Pro 1.4 (Cornell Laboratory of Ornithology, New York) was used to analyse whistle structure. A whistle was defined as narrow-band tonal signal lasting 0.1 s or more, with at least part of the fundamental frequency above 3 kHz (Kriesell et al. 2014). Bottlenose dolphins emit stereotyped whistles known as signature whistles, used to distinguish the emitters. Signature whistles are characterised by the same frequency modulation pattern (called contour), at frequencies ranging between 1 and 38 kHz (Boisseau 2005; May Collado and Wartzok 2008; Hiley et al. 2017) with a duration of between 0.1 and 4.0 s (Buckstaff 2004). Signature whistles can be produced in loops (repetitions of the same elements), usually separated by gaps of less than 250 ms (Esch et al. 2009) and can also have an introductory and/or final loop (Janik and Sayigh 2013), distinct from the central pattern. We considered a unit of analysis any single- or multiple-loop whistle, connected or disconnected (Esch et al. 2009). First, all the whistles were graded on the basis of their signal-to-noise ratio (SNR) as (i) score 1 (whistle visible on the spectrogram but too faint or overlapping with other sounds), (ii) score 2 (whistle clearly visible from its start to its end) and (iii) score 3 (dominant whistle). Only whistles scoring 2 and 3 were analysed further.

In acoustic studies of marine mammals, the observers could easily enter data from the same individuals more than once,

since it is not possible to identify the emitter of sound. This raises issues about pseudo-replication and independence (Hurlbert 1984). Independence of data is one of the assumptions of many statistical methods, thus to reduce the risk of collecting whistles from the same individual and introducing a bias to the sample due to the repetition of many signature whistles (characterised by the same contour), each whistle recognised as a signature whistle by the observer was considered just once in the following analysis. With the aim to identify the signature whistles, we applied the SIGID method based on human observer classification and sequential bout analysis (Janik et al. 2013; Gridley et al. 2014; Kriesell et al. 2014; Hiley et al. 2017). In a bout, whistles with the same contour (modulation pattern) were classified as signature whistles when the bout had at least four whistles in it, and a minimum of 75% of these whistles (within the bout) occurred within 1–10 s of one another. Then, frequency parameters, duration, number of inflection points and number of harmonics were measured by visual inspection of the spectrogram under Raven Pro 1.4 [512/1024-point fast Fourier transform (FFT) and frame length, Hamming window, 50% overlap]. Duration, min, max and frequency range were measured automatically from the selection by Raven, while start and end frequency, number of inflection points and number of harmonics were measured or counted manually. Overall, the dolphin whistle structure was described by eight parameters (Table 2), the response variables of this study.

Table 2 Whistle structure is the result of eight parameters measured on the spectrogram (manually or automatically by Raven Pro 1.4 software)

Parameter	Unit	Description
Start frequency	Hz	The frequency measurement at the start of the whistle.
End frequency	Hz	The frequency measurement at the end of the whistle.
Min frequency	Hz	The lower frequency limit of the selection box.
Max frequency	Hz	The upper frequency limit of the selection box.
Frequency range	Hz	Total bandwidth, calculated by max frequency minus min frequency.
Duration	s	Total duration, calculated by end time minus start time.
Number of inflection points	–	The number of inflection points
Number of harmonics	–	The number of harmonics apart of the fundamental one

Ambient noise

To measure the sea ambient noise (SAN) corresponding to the emission of the whistles, a selection of 5 s immediately before each whistle of good quality (scores 2 and 3) was saved as a wav file and further analysed by means of PAMGuide, a template code provided in R (Merchant et al. 2015). The choice of 5 s was a compromise between the supposed minimum time required to adjust a vocal emission to background noise level in mammals (2 s; Gillam et al. 2007; Hase et al. 2016) and the maximum duration of whistle recorded in the present study (4.3 s). SAN was measured as sound pressure level (SPL). Each selection was described in terms of 1/3 octave bands between 125 Hz and 20 kHz, corresponding to the frequency range of the majority of boat noise (Picciulin et al. 2015; Erbe et al. 2016) and bottlenose dolphin whistles (2–20 kHz, Rako Gospić et al. 2013; Lammers and Oswald 2015; van Ginkel et al. 2017).

Data analysis

Data exploration was carried out following Zuur et al. (2010). Outliers were inspected with Cleveland dot-plots and normality with histograms and Q-Q plots. Conditional scatterplots were used to investigate the potential relationship between the explanatory variables (1) underwater noise (continuous variable, measured as SPL in the 1/3 octave bands centred at 125 Hz, 2000 Hz and 20,000 Hz octave bands), (2) group size (continuous), (3) boat presence (categorical with two levels: no boat; boat), (4) calf presence (categorical with two levels: calf absent, calf present), (5) behaviour (categorical with three levels: feeding, socializing, travelling) and the interactions between noise and boat presence, and group size and calf presence with the response variables (i.e. dolphin whistle parameters). Collinearity between continuous explanatory variables was inspected with pair-plots, and variance inflation factors (VIFs) were calculated. All octave band noise levels were highly correlated with the exception of those centred at 125 Hz, 2000 Hz and 20,000 Hz (VIFs < 2); thus, only these bands were considered in the analysis. Generalised additive models (GAMs), with negative binomial and gamma distributions, were run to correlate separately whistle parameters with the explanatory variables. GAMs are nonparametric extensions of linear regression models that allow the evaluation of highly non-linear relationships between explanatory and response variables thanks to the use of smooth functions (Hastie and Tibshirani 1990). Data explorations indicated to fit noise and group size as smoothed non-linear terms. To avoid over-dispersion, a negative binomial distribution was applied to all whistle parameters, except duration. The choice of the best fitting explanatory variables used in the final model was undertaken using AIC (Akaike information criterion), following a forward selection approach (Zuur et al. 2009).

We started with models with one, two, three and four smoothers; to these models, we added the interaction terms to the smoothers and then the categorical variables. The model with the lowest AIC (Akaike information criterion) was selected (Zuur et al. 2009; see Online Resource SM1). The validation of the fitted model for each whistle parameter was carried out checking for over-dispersion and plotting Pearson residuals against fitted values, against each covariate in the model, and each covariate not in the model (Zuur et al. 2009; Zuur and Ieno 2016; see Online Resource SM2). Finally, temporal autocorrelation among residuals was checked using the autocorrelation function. All analyses were performed using the packages MASS (Venables and Ripley 2002), car (Fox and Weisberg 2011) and mgcv (Wood 2017) in R (R Development Core Team 2015).

Results

The overall dataset consists of 23 h and 22 min of surface behaviour and acoustic recordings collected between 2015 and 2017, during a total of 41 different bottlenose dolphin sightings. From the original sample of 1650 whistles, 330 were considered good quality (score 2 or 3) by the observers. The analysed whistles were extracted from 37 groups among the 41 observed. Based on photo-identification data, we could identify 50 adult individuals, differently associated within the 37 groups. Group size ranged between 3 and 11, with a mean of 6.9 (SD $\pm$ 2.5). Fifty-nine percent of whistles were recorded while calves were present within the group. The analysed whistles were recorded while dolphins were socialising (48%), travelling (30%) and feeding (22%). Resting and milling were not included in the analysis due to the negligible sample size.

SAN (sea ambient noise) levels in the three bands considered in the models (125 Hz, 2000 Hz, 20,000 Hz) ranged, respectively, between (i) 91 and 135 dB re 1 μ Pa (with a mean level of 100 ± 6 dB re 1 μ Pa); (ii) 97 and 150 dB re 1 μ Pa (with a mean level of 112 ± 7 dB re 1 μ Pa); 98 and 127 dB re 1 μ Pa (with a mean level of 108 ± 6 dB re 1 μ Pa). SAN levels increased significantly in presence of boats only in the 125 Hz ($F_{1,328} = 12.52$, $P < 0.0005$) and 2000 Hz ($F_{1,328} = 14.3$, $P < 0.0002$) bands.

GAMs were fitted to 330 whistles. All whistle parameters depended on the specific combination of SPL (sound pressure level) and boat presence and on group size and calf presence (significant correlation with SPL $\times$ boat and group size $\times$ calf), with only two exceptions. In fact, duration was significantly correlated only with the interaction between group size and calf, while the number of inflection points was significantly correlated only with the interaction between SPL and boat (Tables 3 and 4). Noise levels and boat presence changed substantially the whistles parameters. In fact, start and min frequencies increased with the increasing noise at 125 Hz when the

Table 3 Statistical details for smooth and parametric terms of the final GAM models for start, end, min and max frequencies

Start frequency				End frequency			
Smooth term	<i>df</i>	Chi-square	<i>P</i>	Smooth term	<i>df</i>	Chi-square	<i>P</i>
SPL 125 Hz: no boat	1.000	7.001	0.008	SPL 125 Hz: no boat	1.001	1.356	0.244
SPL 125 Hz: boat	1.068	13.357	0.0002	SPL 125 Hz: boat	1.006	4.214	0.040
SPL 2000 Hz: no boat	2.195	6.560	0.0458	SPL 2000 Hz: no boat	2.820	8.196	0.030
SPL 2000 Hz: boat	3.532	9.982	0.0297	SPL 2000 Hz: boat	3.676	10.969	0.022
SPL 20,000 Hz	1.001	0.947	0.3308	SPL 20,000 Hz	2.053	5.231	0.076
Group size: calf absent	5.681	13.653	0.0291	Group size: calf absent	6.325	31.221	< 0.0001
Group size: calf present	6.761	38.853	< 0.0001	Group size: calf present	6.332	30.356	< 0.0001
Parametric terms	Estim.	Std.Err.	<i>P</i>	Parametric terms	Estim.	Std.Err.	<i>P</i>
Intercept	8.9106	0.079	114.293	Intercept	9.279	0.089	104.560
Behaviour (social)	-0.0356	0.089	0.400	Behaviour (social)	-0.146	0.093	0.121
Behaviour (travel)	0.1806	0.100	1.798	Behaviour (travel)	-0.007	0.103	0.946
				Calf	0.147	0.009	1.664
Deviance explained = 23.2% <i>n</i> = 330				Deviance explained = 24% <i>n</i> = 330			
Min frequency				Max frequency			
Smooth term	<i>df</i>	Chi-square	<i>P</i>	Smooth term	<i>df</i>	Chi-square	<i>P</i>
SPL 125 Hz: no boat	1.003	4.415	0.03585	SPL 125 Hz: no boat	1.789	1.764	0.28932
SPL 125 Hz: boat	1.108	11.940	0.00063	SPL 125 Hz: boat	1.023	6.820	0.00916
SPL 2000 Hz: no boat	2.727	8.111	0.03084	SPL 2000 Hz: no boat	2.284	6.209	0.05229
SPL 2000 Hz: boat	3.529	9.702	0.03311	SPL 2000 Hz: boat	4.114	13.980	0.00854
SPL 20,000 Hz	1.004	1.273	0.2596	SPL 20,000 Hz	1.019	3.420	0.06498
Group size: calf absent	6.259	24.107	0.00054	Group size: calf absent	6.600	40.235	< 0.0001
Group size: calf present	6.139	29.107	< 0.0001	Group size: calf present	6.829	44.189	< 0.0001
Parametric terms	Estim.	Std.Err.	<i>P</i>	Parametric terms	Estim.	Std.Err.	<i>P</i>
Intercept	8.7225	0.077	113.282	Intercept	9.4813	0.067	141.926
Behaviour (social)	0.0186	0.089	0.207	Behaviour (social)	-0.1335	0.078	0.086
Behaviour (travel)	0.1654	0.100	1.648	Behaviour (travel)	0.0327	0.086	0.704
Deviance explained = 24.1% <i>n</i> = 330				Deviance explained = 27.4% <i>n</i> = 330			

SPL sound pressure level, “.” = interaction
Significant terms are in *italics*

Table 4 Statistical details for smooth and parametric terms of the final GAM models for frequency range, duration, number of inflection points and number of harmonics

Frequency range		Duration		Number of inflection points		Number of harmonics	
	<i>df</i>	Chi-square	<i>P</i>		<i>df</i>	Chi-square	<i>P</i>
Smooth term				Smooth term			
SPL 20,000 Hz	1.013	5.001	<i>0.026</i>	SPL 125 Hz: no boat	1.950	0.493	0.616
Group size: calf absent	6.738	26.769	<i>0.003</i>	SPL 125 Hz: boat	3.808	1.491	0.181
Group size: calf present	5.534	20.185	<i>0.002</i>	SPL 2000 Hz: no boat	1.000	0.001	0.979
Parametric terms	Estim.	Std.Er.	<i>Z</i> -value	SPL 2000 Hz: boat	1.990	1.337	0.287
Intercept	8.749	0.108	81.092	SPL 20,000 Hz: no boat	1.000	1.649	0.200
Behaviour (social)	−0.189	0.117	−1.621	SPL 20,000 Hz: boat	7.847	1.586	0.099
Behaviour (travel)	−0.162	0.122	−1.335	Group size: calf absent	6.925	3.980	<i>0.0007</i>
Calf	0.195	0.102	1.916	Group size: calf present	1000	2.253	0.134
				Parametric terms	Estim.	Std.Er.	<i>t</i> -value
				Intercept	0.670	0.066	10.202
				Boat	0.198	0.082	2.407
							<i>P</i>
							< <i>0.0001</i>
							<i>0.0167</i>
Deviance explained = 16% <i>n</i> = 330							
Number of inflection points							
Smooth term	<i>df</i>	Chi-square	<i>P</i>	Smooth term	<i>df</i>	Chi-square	<i>P</i>
SPL 125 Hz: no boat	1.000	1.617	0.20366	SPL 125 Hz: no boat	2.194	2.318	0.33398
SPL 125 Hz: boat	4.472	10.461	<i>0.04415</i>	SPL 125 Hz: boat	1.000	4.414	<i>0.03566</i>
SPL 2000 Hz: no boat	1.687	0.307	0.75049	SPL 2000 Hz: no boat	1.495	2.536	0.14065
SPL 2000 Hz: boat	1.000	1.144	0.28477	SPL 2000 Hz: boat	1.001	0.038	0.84640
SPL 20,000 Hz: no boat	1.000	0.392	0.53154	SPL 20,000 Hz	4.809	9.995	0.06755
SPL 20,000 Hz: boat	1.000	8.094	<i>0.00444</i>	Group size: calf absent	6.010	17.921	<i>0.00669</i>
Group size	2.737	1.524	0.47738	Group size: calf present	6.660	23.995	<i>0.00078</i>
				Parametric terms	Estim.	Std.Er.	<i>Z</i> -value
				Intercept	0.0447	0.1347	0.332
				Calf	−0.1903	0.2390	−0.797
							<i>P</i>
							0.740
							0.426
Deviance explained = 10.4% <i>n</i> = 330							

SPL sound pressure level, “.” = interaction

Significant terms are in italics

boats were present, while they decreased with the increasing noise when the boats were absent; end and max frequencies, the number of harmonics and the number of inflection points increased with the increasing noise at 125 Hz when the boats were present, while they were not correlated to noise when the boats were absent; min and end frequencies increased with the increasing noise at 2000 Hz when the boats were absent, while when the boats were present, start, min, end and max frequencies decreased when the noise at 2000 Hz was higher than 120 dB re 1 μ Pa (Tables 3 and 4, Fig. 2). Overall, the number of inflection points and frequency range significantly increased with the increasing noise at 20,000 Hz, and at the end, duration increased in the presence of boats, independently of the noise level (Tables 3 and 4, Fig. 2). All whistle parameters, except number of inflection points and duration, were correlated with the interaction between group size and calves; namely, in the presence of calves, they remained approximately stable for small (3–4 animals) or large group size (10–11 animals) and decreased or increased for medium-sized group (from 5 to 9 animals, Fig. 3), while in the absence of calves, they remained approximately stable. The only exception was duration, which was correlated with group size only in the absence of calves (Fig. 3).

All the frequency parameters were significantly correlated with behaviour: start and min frequencies were lower during feeding than during social and travelling, while end frequency, max frequency and frequency range were higher during feeding than during social and travelling (Tables 3 and 4, Fig. 4). However, no correlation was found between behaviour and the other whistle parameters (duration, number of inflection points and number of harmonics; Table 4).

Discussion

Variables influencing whistle structure

Significant changes in the acoustic structure of bottlenose dolphin whistles were mainly due to the interaction between noise level and boat presence, group size and calf presence and behavioural context. Particularly, the acoustic response to noise varied depending on whether boats were present or not, at least in the lower bands. In the presence of boats, dolphins appeared to increase their whistle frequencies and the number of harmonics as a function of increasing noise in the band centred at 125 Hz. In addition, dolphins tend to increase and then either maintain or reduce whistle frequencies as a function of increased noise in the band centred at 2000 Hz. In the absence of boats, minimum and start frequencies decreased with increasing noise in the band centred at 125 Hz, while minimum and end frequencies increased with increasing noise in the band centred at 2000 Hz. Frequency range and the number of inflection points increased only when noise increased in the highest

band (centred at 20,000 Hz). The observed increase in fundamental frequencies was more pronounced when noise levels were higher in the band centred at 125 Hz. We exclude that this result is an artefact of measurement errors due to masking from boat noise. In fact, duration, number of inflection points and frequency range were not reduced by the increased low-frequency noise, as it was found by Heiler et al. (2016). Moreover, for equal levels of noise, the fundamental frequencies increased with the increasing noise only when boats were present, while they were reduced or not affected when the boats were absent. Bottlenose dolphins produce whistles with energy mostly between 2 and 20 kHz (Richardson et al. 1995), but they are also able to hear sounds at 100 Hz and produce sounds at 200 Hz (Turl 1993; Schultz et al. 1995; Herzing 1996). The observed shifted frequencies in conditions of elevated low-frequency noise has already been detected in other studies (May Collado and Wartzok 2008; Luís et al. 2014; Rako Gospić and Picciulin 2016). In addition, noise level at 125 Hz was an effective indicator of boat noise, one of the most common anthropogenic noise sources in coastal environments (Picciulin et al. 2015), and it can be used to predict the effect of noise on the acoustic structure of bottlenose dolphin whistles (Rako Gospić and Picciulin 2016).

The observed response to high noise levels, which is to increase whistle frequencies, may be interpreted as the animal's attempt to efficiently transmit information acoustically despite the degraded acoustic environment. Higher frequency sounds may be localised more easily in the short distance, as they attenuate more quickly in the ocean (Hefner and Hefner 1992). Alternatively, the observed increase in whistle frequencies could be related to the Lombard effect already demonstrated in mammals and birds (Brumm and Zollinger 2011) and together with the increase in the amplitude of the whistles, serve as a mechanism to compensate for the masking due to high noise levels (Holt et al. 2009; Parks et al. 2011).

The majority of whistle parameters correlated significantly more with noise when boats were present. In addition, in accordance with the results of other studies (La Manna et al. 2013; May Collado and Quinones-Lebron 2014; Rako Gospić and Picciulin 2016), whistle duration changed in the presence of boats, independently of the noise levels. Two possible scenarios are to be considered: boats can be perceived as a threat, as their presence may induce stress in dolphins (Frid and Dill 2002), or boats determine an increase in the level of dolphin arousal (Hawkins and Gartside 2010). However, both situations, stressful conditions and increased arousal, have already been found to promote longer and higher frequency sound emissions in dolphins as in other species (Wiener et al. 1990; Monticelli et al. 2004; Esch et al. 2009; Briefer 2012). Nevertheless, our results indicate that the acoustic reaction of dolphins to boats is the result of a complex interaction between the physical presence of boats and the noise they produce (Ellison et al. 2012), highlighting the need to consider

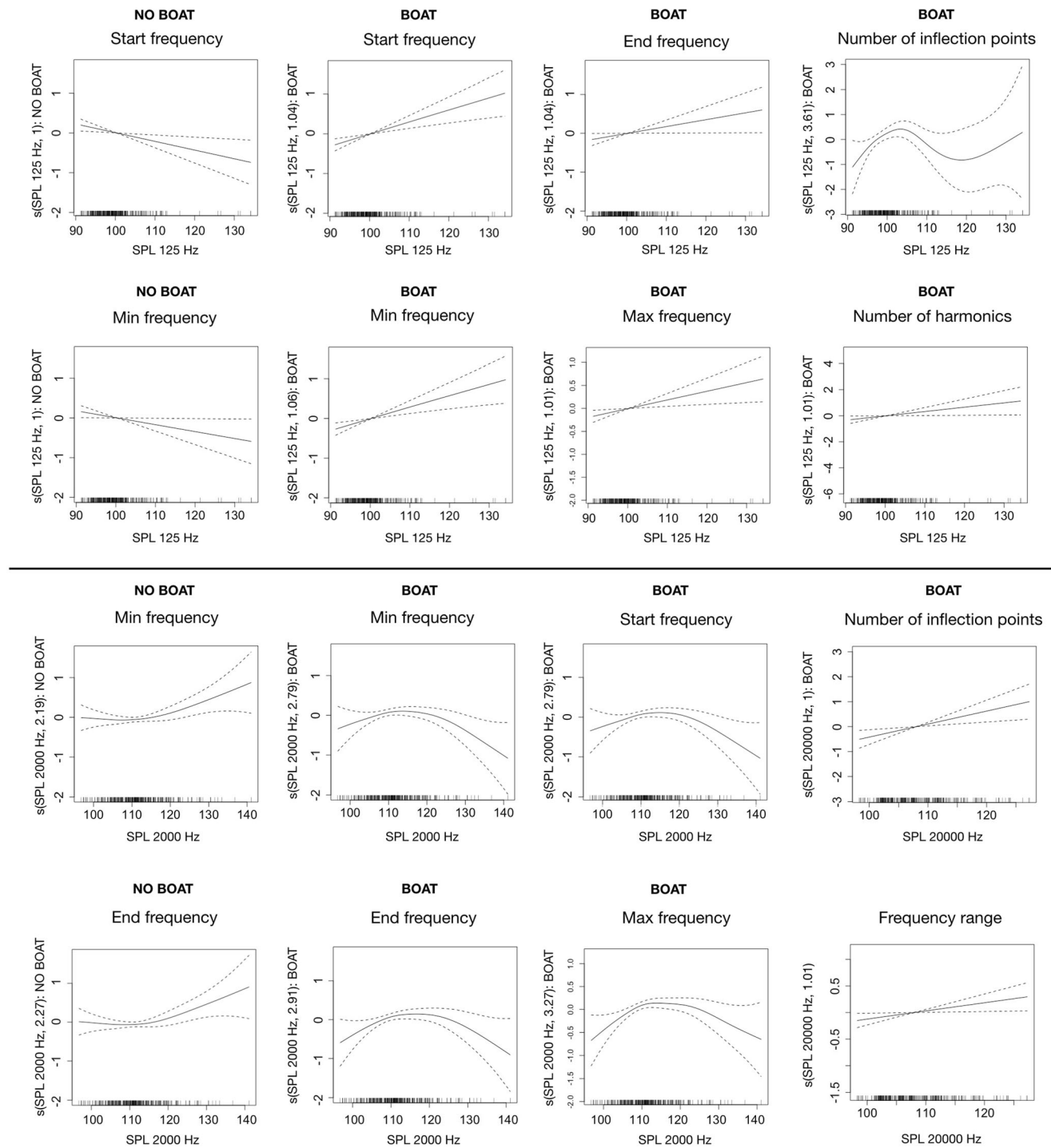


Fig. 2 Summary of GAM results showing only the significant explanatory variables of the models: either the interactions between boat (presence vs absence) and noise (SPL in 125 Hz, 2000 Hz and 20,000 Hz bands) or noise (SPL in 20,000 Hz) itself. The y-axis represents the additive predictor by GAM, which is a smoothed

function for each explanatory variable or for each of their interactions, and it explains the effect on frequency parameters (start, end, min and max frequencies, frequency range, number of inflection points, number of harmonics). SPL = sound pressure level; “:” = interaction. The solid line is the smoother and the dotted lines are 95% point-wise confidence bands

both these factors when analysing the disturbance effect of boat traffic on dolphin behaviour. Because these mechanisms of effects were not investigated in the present study, they need further investigations.

Regarding the effect of the other explanatory variables tested, social factors (group size and calf presence) affected all whistle parameters, excluding only the number of inflection points. Frequency parameters changed more as a function of

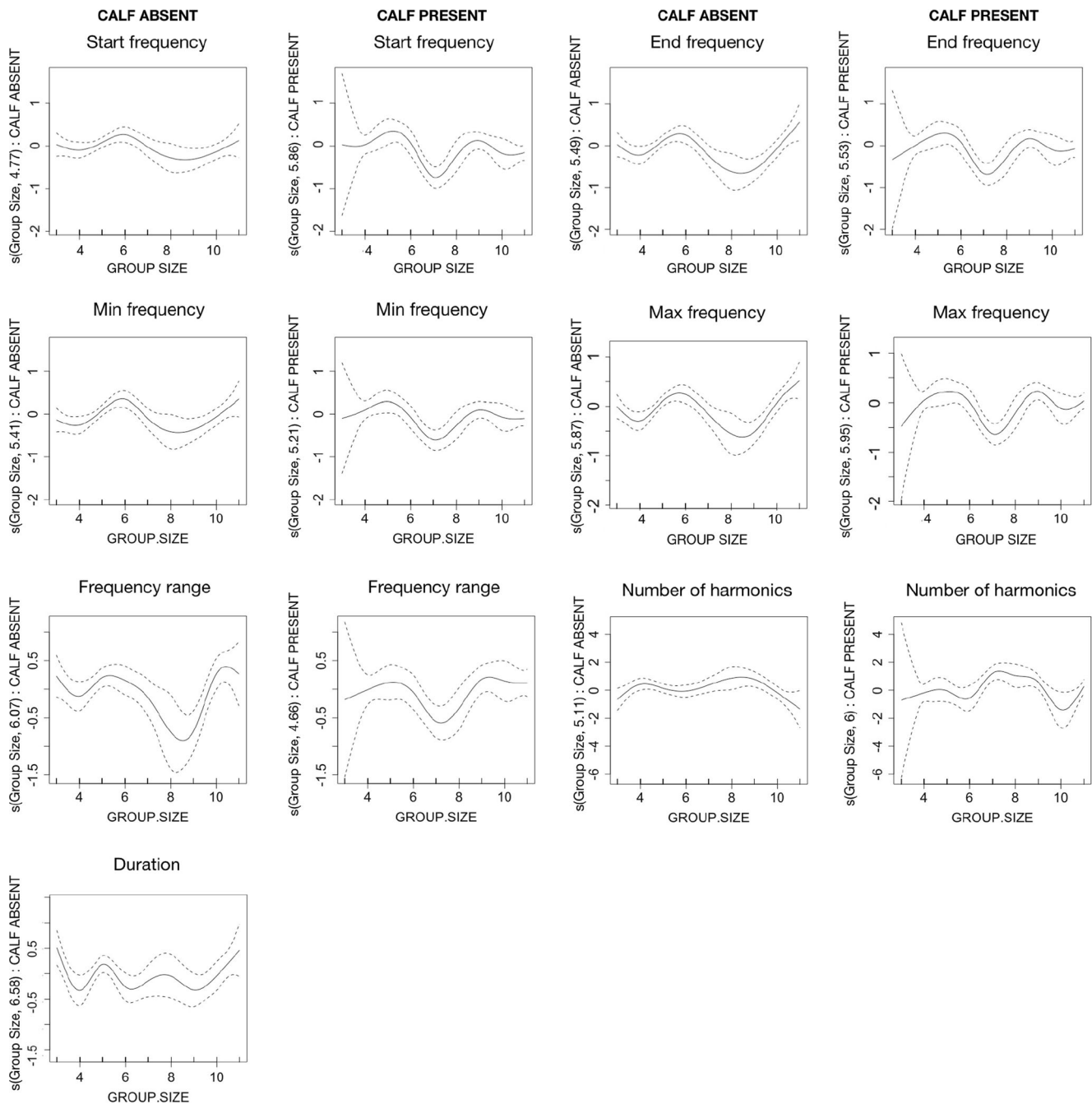


Fig. 3 Summary of GAM results showing only the significant explanatory variables of the models: the interaction between group size and calf presence. The y-axis represents the additive predictor by GAM, which is a smoothed function for the interaction between group size and

calf presence, and it explains the effect on frequency parameters (start, end, min and max frequencies, frequency range, duration, number of harmonics). “:” = interaction. The solid line is the smoother and the dotted lines are 95% point-wise confidence bands

group size in the presence of calves than in the absence of calves, and particularly when the groups were medium size. The variable pattern of whistle frequency change in relation to calf presence and group size is not easily explainable (Heiler et al. 2016) since it is not possible to separate the influence of calf whistles on the total samples. Calf whistles are not as complex as most adult whistles (Caldwell and Caldwell

1979), and neonate bottlenose dolphins use mimicry and over produce a variety of whistle segments in effort to achieve a stereotyped adult-like whistle (Tyack and Sayigh 1997). During the first months of the calf’s life, the mother apparently whistles frequently to produce a whistle model in which the calf can imitate; these whistles were frequently followed by the newborn’s whistle (Janik 2000). Moreover, whistles can

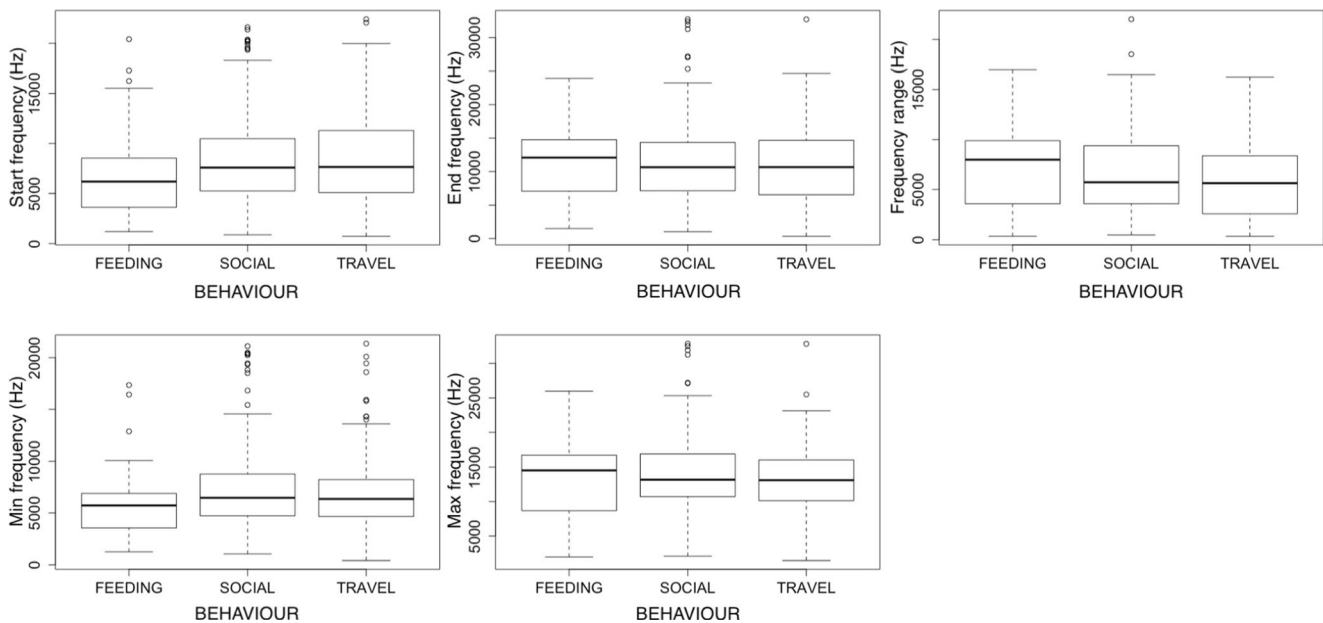


Fig. 4 Summary of GAM results showing only the significant parametric terms, behaviour (feeding, social and travel). It explains the effect of behaviour on start frequency (Hz), end frequency (Hz), frequency range (Hz), min frequency (Hz), max frequency (Hz). The thick black lines

represent the medians, the boxes encompass the 25% and 75% quartiles, the whiskers extend to the most extreme data points within 1.5× the interquartile range outside the box, and the circles show data points beyond the whiskers

communicate calf emotion (e.g. fear or stress), and this in turn can be responsible for changes in the mothers' whistles (Smolker et al. 1993; Mello and Amundin 2005). Thus, a lot of concomitant factors (e.g. number and age of the calves, their emotional state, the position relative to the mother) can be responsible for the pattern observed, and this aspect needs further investigation to be clarified.

The number of harmonics increased when calves were present if the group was composed of more than six individuals. Harmonics are the result of a deviation of a whistle's waveform from the pure sinusoidal (Au and Hastings 2008); whether that is a voluntary by-product of whistle production, or whether dolphins can voluntarily define and control whistle form during its production is still unclear (Lammers and Oswald 2015). It has been proposed that harmonics can transmit information related to the direction of movement and changes in orientation (Miller 2002; Lammers and Au 2003; Branstetter et al. 2013); if true, the observed increase in whistle harmonics could be useful in providing calves with more information on the direction of adult individual movements in larger groups. However, the number of harmonics can also be influenced by the position and the distance of the animals with respect to the hydrophone. Lammers and Au (2003) found that whistles from spinner dolphins swimming toward the array of hydrophones contained more harmonics than those from dolphins moving in opposite direction. Rasmussen et al. (2006) found that in white-beaked dolphins, the number of harmonics decreases with the increasing distance. Considering that in the present study, the position of the animals with respect to the hydrophone was not measured, our result should be

interpreted with caution and further investigation are necessary to understand the role of harmonics.

Considering behavioural context, feeding was the only behavioural state that influenced the whistle structure, while no changes were observed between travelling and socialising. When feeding, bottlenose dolphins whistle with lower min and start frequencies but with higher max, end frequencies and frequency range. Skeyrms (2009) suggested that in the presence of multiple senders and receivers, a network signalling may facilitate group decision making and coordinate collective action. Recent studies found a similar shift in whistle frequencies during behavioural states characterised by a high level of arousal such as feeding (e.g. Acevedo-Gutiérrez and Stienessen 2004; Hawkins and Gartside 2010; La Manna et al. 2013; May Collado and Quinones-Lebron 2014; King and Janik 2015; Rako Gospić and Picciulin 2016). Foraging is a challenging task requiring a high level of coordination between group members; this is achievable through whistle adaption. In other behavioural contexts, such as socialising and travelling, dolphins may prefer to adopt different strategies to remain in contact with other group members. For example, in the case of social interactions, dolphins may need less acoustic communication since they are engaged in intimate behaviours and physical interactions involving tactile information exchange (May Collado and Quinones-Lebron 2014). As an alternative, dolphins may change the whistle repetition rates rather than changing the acoustic properties of their whistles during socialising (Cook et al. 2004; Díaz López and Shirai 2009; Quick and Janik 2008; Guerra et al. 2014). Nevertheless, in other

cases, a variation in whistle parameters during socialising was also detected (Rako Gospić and Picciulin 2016; Heiler et al. 2016), suggesting a high plasticity of dolphin whistles and their context-dependent adaptation.

Methodological concerns

The adaptation of bottlenose dolphin whistles investigated worldwide has led to seemingly inconsistent results, especially for some of the commonly considered acoustic parameters. This could be a result of neglecting sources of variability that could have confounding effects on the whistle structure. Our results support the hypothesis that the acoustic strategy adopted by bottlenose dolphins to ensure efficient transmission of their own signals depends on the soundscape of the habitat and the predominant nature of the noise (environmental or anthropogenic). Moreover, results emphasise the need to simultaneously consider multiple variables when investigating whistle parameters, as the species is capable of adopting different acoustic communication strategies depending also on the complex interaction between social and behavioural context.

However, as a further explanation of the results' inconsistencies, we identify some methodological issues and potential sources of variability, and thus misleading conclusions. Because whistle parameters depend on the aggregation of individuals and their actions, the need to detect the activity of specific individuals arises. In other words, when considering the predominant activity of the group, few animals could perform activities different from the majority without being detected, whilst diving for example. However, with the equipment commonly used in this field, it is not possible to discriminate the emitter of the signals. Therefore, the risk of attributing acoustic data to the wrong behavioural observations may exist, leading to ambiguity in interpretation of the results (Díaz Lopez 2011; Marley et al. 2017).

Another important methodological issue concerns the influence of signature whistles. When considering signature whistles multiple times, the response of a specific individual can be oversized with respect to the other group members. In marine mammals, studies on the effect of noise have generally considered the overall group response, mainly due to methodological constraints. Nevertheless, studies on other animals (e.g. fish) have already identified the inter-individual variability of response to noise (Radford et al. 2015; La Manna et al. 2016) and Lusseau (2003) demonstrated that the response of bottlenose dolphins to boat disturbance changes between males and females. Moreover, the possibility that the response observed may concern only some individuals in particular motivational or physiological states or individuals that already experienced or not experienced encounters with this specific stressor (Blumstein 2006) should be taken into consideration when generalising the obtained results.

Lastly, our models explained less than 30% of the deviance, meaning that other variables which we did not consider

in this study could influence whistle structure. For example, the masking effect of boat noise can also depend on the number and position of boats in relation to the dolphin group, the type of boat with its specific engine noise characteristics and boat speed and direction of movement. In addition, the response to boat noise can be influenced by the animal's previous experience with this anthropogenic sound, independently of the received sound level (Ellison et al. 2012). Lastly, the communication network in which the signal is emitted should be considered; thus, not only the number of individuals but also their identity and relations can aid understanding of whistle variability (Fichtel and Manser 2010).

Conclusions

Currently, literature reports on the varying changes in vocal behaviour of bottlenose dolphins in relation to boat presence, noise and behaviour. However, little attention has been paid to the combined effect of several variables, and to our knowledge, this is one of few studies to deal with this issue. In addition, this study provides an indication of the vulnerability of bottlenose dolphin communication to acoustic pollution within a small population. These findings highlight the need for further investigation of the effects of various type of noise on whistle structure, as well as the consistency of response patterns across different populations. Understanding how communication systems function is essential when studying animal behaviour and the ecology of species, as interactions between individuals are mediated mainly by vocal signals (Bradbury and Vehrencamp 1998). Vocal signals have been found to play a crucial role in determining the outcome of intra- and inter-sexual competition, in mediating agonistic or affiliative interactions between individuals (Fitch and Hauser 2002), and in coordinating individuals against predators (Owings and Morton 1998). Therefore, it is important to further investigate this issue to evaluate the effects of the changes in bottlenose dolphin whistling as an adaptation to anthropogenic noise on the species' fitness, and predict how these alterations will interfere with effective conservation of the species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This work was approved by MareTerra Onlus, University of Sassari and Blue World Institute. All procedures performed in the study were in accordance with the ethical standards of the involved institution.

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